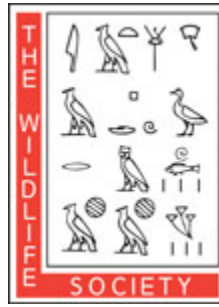


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FEEDING BEHAVIOR AND HABITAT SELECTION OF MULE DEER AND ELK ON NORTHERN UTAH SUMMER RANGE

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Abstract: The feeding behaviors and habitat preferences of tame, free-ranging mule deer (*Odocoileus hemionus hemionus*) and elk (*Cervus elaphus nelsoni*) were determined in quaking aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) types. Mule deer and elk exhibited strong grazing preference for open habitat subunits. Elk most preferred highly productive meadow bottoms, whereas deer most preferred less productive clear-cut lodgepole pine and aspen forest. Clear-cutting greatly increased deer and elk grazing use of these areas in the lodgepole pine type, but aspen clear-cuts were used at about the same level as uncut aspen. The lack of mule deer use of meadow bottoms was attributed to their need for a more digestible diet. Mule deer were generally more selective than elk, especially in meadow subunits, where density of vegetation and abundance of nonpreferred grasses and sedges apparently interfered with forage selection and prevented maximum forage consumption rates. Elk were apparently better adapted than deer to using a more diverse array of plant species as food. Consumption rates were highest on subunits the animals most preferred to graze. That both species made considerable use of less preferred habitat, where consumption rates were relatively low, suggests that deer and elk are innately motivated to explore their environments for alternate food resources. Elk generally preferred to bed wherever they finished feeding, although always in close proximity to cover. Mule deer generally retreated to specific beds that they used repeatedly throughout the summer.

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Animal preferences for habitat characteristics are not uniform, and subsequently neither are the benefits of habitat management practices the same under all conditions (Pengelly 1972). Deer and elk, for example, may make considerable use of riparian areas and clear-cuts where forage is of better quality and/or more abundant, but avoid such areas if human disturbance exceeds a certain threshold (Black et al. 1976, Hershey and Legee 1976, Lyon and Jensen 1980); they may avoid areas within 200 m of open roads (Rost and Bailey 1979), but use closed roads as travel routes or preferred foraging sites (Marcum 1975, Collins et al. 1978). Not only are big game preferences diverse, but interactions of factors such as

cover, snow depth, topography, human activities, and forage quality and quantity may confound assessment of actual requirements (Peek et al. 1982).

The objective of this study was to evaluate the relative importance of subunits of the aspen and lodgepole pine types to mule deer and elk. This study was supported by the Utah Division of Wildlife Resources through Federal Aid to Wildlife Restoration Project W-105-R and the Utah Agricultural Experiment Station, Utah State University. The U.S. Forest Service, Intermountain Forest and Range Experiment Station provided partial funding, materials, and use of sites. The University of Alaska Agricultural Experiment Station supported manuscript preparation and publication. We thank J. Malechek, W. Mueggler, B. Gilbert, I. Dirmhirn, and the referees for their comments.

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STUDY AREAS

The study was conducted in the lodgepole pine and aspen vegetation types. The lodgepole pine study area was on the Little Brush Creek drainage of the Ashley National Forest. Almost 90% of the area has a lodgepole pine overstory, of which 70% was stagnated forest and nearly devoid of understory. Less than 3% of the stagnated forest was clear-cut in 1960, and is now dominated by 1–2-m saplings with a moderately productive understory. The remainder of the area consisted of wet and dry meadows containing a diverse and highly productive array of forage species. Detailed description of this area was given by Collins et al. (1978).

The aspen study area was centered on the Chicken Creek drainage of the Davis County Experimental Watershed, 8 km east of Farmington, Utah. Fifty-seven percent of this area was aspen forest that had a diverse and highly productive understory. Approximately 8% was clear-cut in 1974, with the slash being cleared from most areas. The understory vegetation in the clear-cuts was similar to that in uncut areas, but total production was greater and dominated by 1–2-m aspen sprouts after 3 years. Stands of mountain brush, dominated by mountain snowberry (*Symphoricarpos oreophilus*) and common chokecherry (*Prunus virginiana*), covered 10% of the area. The remainder was occupied by meadow, grading into riparian vegetation. A more detailed description of the area was presented by Johnston and Doty (1972) and Collins (1979).

METHODS

Observations of free-ranging, tame mule deer and elk formed the basis of this study. The deer and elk were obtained as fawns

and calves from the Utah Division of Wildlife Resources. They were fed fresh goat's milk the 1st 5 to 6 weeks, then weaned and maintained on alfalfa (deer), native grass hay (elk), and rolled barley. Field observations were only made of yearling or adult animals.

Neff (1974) suggested that maintenance of tame deer in pens off the study area led to inefficient grazing and unsettled preferences during diet observation trials. Consequently, enclosures of slightly more than 2.5 ha were built on the study areas to encompass habitats representative of those to be sampled. The enclosures also served to maintain the animals during nonsampling periods, providing sufficient feed until the last 2 or 3 weeks of the study periods, at which time the diet was supplemented with hay.

Scan sampling, a technique described by Altmann (1974), was used to determine the time deer and elk spent grazing, resting, ruminating, traveling, standing, sleeping, and playing on each of the habitat subunits in both types. Observation periods lasted 24 hours and the location and activity or state of each animal was noted at 10-minute intervals. Elk were observed in groups of 5 to 7 biweekly throughout the summers of 1977 and 1978 in the aspen type and biweekly during the summer of 1976 in the lodgepole pine type (Collins et al. 1978). Mule deer were observed individually or in pairs because they are not gregarious during the summer. Scan samples of deer were obtained on alternate weeks from those of elk in summer 1977 and 1978 in the aspen type and summer 1978 in the lodgepole pine type.

Night observations were made with the aid of a flashlight. A pen light was attached to the collar of 1 animal to facilitate following the animals without the use

of a flashlight. Neither light had any noticeable effect on animal behavior. At least 1 animal was equipped with a radio transmitter to aid in locating the animals when the observer occasionally became separated from them.

The relative amount of each habitat subunit available to the animals was determined by connecting the points of maximum peripheral deer or elk movement as recorded over the entire summer and taking 900 point samples on aerial photographs covering the same area. Percent availability was calculated directly from the point distribution.

Forage production on meadow, logging road, and mountain brush subunits of the aspen type was determined by use of a double-sampling technique (Wilm et al. 1944). Weight estimates were made on 120 20 × 50-cm plots in each subunit. One of every 5 plots was clipped for actual dry-weight determinations. The clipped weights were used to adjust the estimates by regression analysis. Forage production estimates in the remainder of the aspen subunits and all of the lodgepole pine subunits were determined concurrently by similar techniques by personnel of the U.S. Forest Service, Intermountain Forest and Range Experiment Station, and Utah Division of Wildlife Resources.

Diet sampling was conducted from mid-June to mid-September in both types. In the lodgepole pine type, deer diets were sampled in 1976 by Deschamp (1977) and diets of elk were sampled by Collins (1977). Deer and elk diets in the aspen type were sampled in 1977 by Collins (1979). In the lodgepole pine type, dietary information was obtained by individually observing 3 cows, 3 castrates, and 1 bull elk and 4 female and 1 castrate deer. In the aspen type, observations were made of 2 cows, 2 castrates, and 1 bull elk and 4 female deer. The bite-count technique

was used as described by Wallmo and Neff (1970), except animals were not restrained during sampling. All dietary information was estimated on a species dry-weight basis. Samples of equal size (observation time) were obtained for each animal, week, and subunit in the lodgepole pine type. However, in the aspen type, the animals were observed only as they voluntarily entered each subunit, resulting in unequal sampling times. Seventy-five to 150 bites (simulated by hand-clipping) of each species in each diet were collected, oven-dried, and weighed to form the basis for weighting bite-count totals. Initially, simulated bites were collected biweekly on all species; thereafter, they were collected only on species actively growing. Consumption rates were calculated as the average dry-weight consumption per minute of grazing during the period of diet sampling.

Diets were composited from plant species hand-clipped to be representative of plant parts consumed by the animals. Plants were collected for each period in which diets were determined. Plants were oven-dried at 60 C and ground to pass a 40-mesh screen. Ground material was combined with other dietary species in the same proportion as found in average deer and elk diets for each sampling period.

The Tilley and Terry (1963) *in vitro* organic-matter digestibility (IVOMD) determination was used to estimate the digestibility of the composited diets. Inoculum for the procedure was obtained from animals grazing the aspen type. A vacuum aspiration hand pump and flexible plastic tube was used to extract rumen fluids via the esophagus. The experimental animals were tranquilized with Rompun (Haver-Lockhart Laboratories, Shawnee, Kans.) during this procedure. Inocula for the 1st 2 deer periods were obtained from wild deer killed in the same area. In both cases,

Table 1. Mule deer and elk use (%) of aspen and lodgepole pine types in northern Utah. Sample sizes are in parentheses.

Type and subunit	Percent total area used		All activities		Grazing		Resting	
	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk
Aspen	(900)	(900)	(996)	(3,088)	(386)	(1,120)	(516)	(1,496)
Aspen forest	56.6	56.6	58.7	20.5---**b	45.3--	17.9---**	70.7++	14.7---**
Clear-cut	7.9	7.9	2.2	4.1*	4.1-	7.0*	0.8--	1.6--
Conifer	3.2	3.2	0.1--	0.6--	0.0--	0.0-	0.0--	0.0-
Logging road	0.5	0.5	1.0	2.3*	1.6+	3.2++	0.0	0.0
Meadow	14.4	14.4	31.2++	68.4+++*	35.2++	65.3+++*	28.5++	83.2+++*
Mountain brush	17.5	17.5	6.7--	4.0---**	13.7	6.7---**	0.0-	0.5--
Lodgepole pine	(900)	(900)	(672)	(4,662)	(310)	(2,307)	(276)	(2,355)
Wet meadow	3.0	2.7	14.8++	46.8+++*	30.6++	43.6+++*	0.0-	50.5+++*
Dry meadow	1.2	11.7	1.4	20.6+++*	3.0+	33.6+++*	0.0	15.6+++*
Clear-cut	4.9	4.4	24.8++	8.4+++*	36.3++	14.6+++*	4.1	0.7---**
Mature forest	13.3	11.9	10.0-	12.4	13.0	3.3---**	8.1-	20.7+++*
Revegetated road	77.0	68.7	0.0-	1.9*	0.5	3.0+++*	0.0	0.0--
Stagnated forest	0.6	0.6	48.9--	9.8---**	16.6--	1.9---**	87.8++	12.7---**

a All activities combined include traveling, grooming, standing, and drinking, as well as grazing and resting.
b z test for significance: - or + indicates animal use was less or greater than availability, $P < 0.01$; -- or ++ indicates significance at $P < 0.001$; * and ** indicate deer vs. elk use of a subunit for the activity differed at $P < 0.01$ and $P < 0.001$, respectively.

the inocula were maintained under anaerobic conditions at 39 C and transferred to the laboratory within 2 hours. Inocula from both deer and elk were used in the fermentation of both species' diets. The macro-Kjeldahl procedure (Harris 1970) was used to analyze representative diets for crude protein content (percent nitrogen $\times 6.25$).

Habitat use : availability data were analyzed by the z test for significance of a binomial proportion (Snedecor and Cochran 1972). This test was also used to determine differences between deer vs. elk habitat subunit preferences. Diet selectivity and overlap were calculated by use of the percentage similarity equation (Whittaker 1975), comparing species composition of diet to species composition of the community. High values indicate greater overlap of dietary composition with community composition and, hence, lower selectivity than indicated by smaller values. Dietary overlap between deer and elk was also determined in this way. The Friedman 2-way analysis of variance by ranks

(Siegel 1956) was used to test for differences in selectivity between deer and elk, because expression of greater selectivity by either animal is likely not an interval measure of strength.

Principal species are defined as species representing more than 5% of a diet. Subunit is defined as a division or segment of the general habitat and is based on major differences in vegetation cover and dominance.

RESULTS

Habitat Use

The relative proportions of the different subunits used by mule deer and elk in the aspen type were the same. Proportions used by the 2 species in the lodgepole pine type, however, were quite different because deer did not range over the same area as elk (Table 1).

In the aspen type, both deer and elk grazed logging road and meadow subunits more ($P < 0.01$) than their availability overall (Table 1). Elk grazed the meadow

Table 2. Production (%) by forage class on different habitat subunits in the aspen type, Wasatch Mountains, Utah, and the lodgepole pine type, Uinta Mountains, Utah.

	Aspen subunits					Lodgepole pine subunits				
	Aspen	Clear-cut	Logging road	Meadow	Mountain brush	Riparian	Wet meadow	Dry meadow	Clear-cut	Mature forest
Forbs	54.4	44.8	64.2	54.5	26.8	53.3	18.0	45.3	47.5	3.8
Grasses and sedges	32.1	29.0	33.0	43.8	18.2	42.8	80.8	54.7	36.5	2.6
Browse	13.5	26.2	2.8	1.7	55.0	3.9	1.2	0.1	16.1	92.5
Mushrooms							0.1	0.1	0.1	1.1
Total production (kg/ha)	1,774	3,043	1,245	2,155	1,570	2,820	2,664	1,148	484	335
										37

almost twice as much as deer, and deer grazed in the forest more than twice as much as elk. If preference is considered to be proportional to the total time the animals grazed each subunit, mule deer preferred to graze the aspen foremost and the meadow secondarily. Elk exhibited the opposite preference. Deer and elk grazing preferences differed ($P < 0.01$) on all subunits except the logging road and conifer subunits.

Deer and elk both used the aspen and meadow (in aspen type) subunits as resting areas more ($P < 0.01$) than their availability, while using the other subunits less ($P < 0.01$) (Table 1). Deer showed greater preference for resting in aspen stands than did elk. Elk, however, showed much greater preference than deer for resting in the meadow subunit. When deer and elk rested in the meadow subunit, they were generally within 2–3 m of cover; this cover usually consisted of riparian aspen or alder (*Alnus* spp.) stands. Resting area preferences of deer and elk were different ($P < 0.01$) only in the aspen and meadow subunits.

In the lodgepole pine type, both deer and elk grazed wet meadow, dry meadow, and clear-cut subunits more ($P < 0.01$), and grazed stagnated forest less ($P < 0.01$) than their availability (Table 1). Deer grazed the clear-cut preferentially and the wet meadow secondarily. Elk preferred grazing wet meadow, dry meadow, and clear-cut, in that order. Deer preferred grazing the forested segments much more than elk and dry meadows much less than elk. Differences between deer and elk grazing use of the lodgepole pine subunits were significant in all instances (Table 1).

Mule deer rested in stagnated forest more ($P < 0.01$) and the wet meadow and mature forest less ($P < 0.01$) than their availability. Elk used wet meadows, dry

Table 3. Dry weight production (kg/ha) of forage classes and principal species occurring in deer and/or elk diets on cut and uncut aspen and lodgepole pine stands in northern Utah.

Forage classes or species	Aspen type				Lodgepole pine type			
	Aspen		Clear-cut		Lodgepole pine		Clear-cut	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Forbs	965	174 a*	1,364	142 b	6.6	2.4 c	307.8	51.4 d
Grasses and sedges	569	169 a	882	173 b	2.7	1.4 c	138.6	43.1 d
Browse	240	90 a	797	257 b	16.9	9.8 c	76.3	55.9 d
Bearded wheatgrass	67	10 a	426	53 b				
Mountain brome	346	105 a	389	81 a				
Quaking aspen	17	18 a	268	63 b				
Snowberry	175	96 a	504	222 b				
Engelmann aster	45	29 a	58	26 a				
American vetch	114	50 a	133	44 a				
Western valerian	175	74 a	230	54 a				
Mushrooms					10.2	5.0 a	0.0	0.0 b
Heartleaf arnica					3.1	1.2 a	1.1	0.4 b
Pacific aster					0.1	1.0 a	11.8	5.2 b
Milkvetch					0.1	0.9 a	92.9	42.9 b
Goldenrod					0.3	1.0 a	29.8	9.8 b
Dandelion					0.0	0.0 a	34.2	5.3 b
Carex spp.					2.2	1.4 a	89.0	17.2 b
Aspen					0.4	1.1 a	73.1	56.0 b
Grouse whortleberry					15.1	8.9 a	0.1	0.7 b

* Means within rows followed by a common letter are not different ($P < 0.05$).

meadows, and mature forests as resting areas more ($P < 0.01$) than their availability, while using clear-cuts, revegetated roads, and mature forest less ($P < 0.01$) than availability (Table 1). Mule deer obviously preferred resting in the stagnated forest subunits, whereas elk preferred to rest in the wet meadow. Dry meadow and mature forest were also preferred as resting sites by elk, but much less than the wet meadow. Resting-area preferences of deer and elk differed ($P < 0.01$) in all instances except revegetated roads (Table 1).

Forage Production

In the aspen type, forage production almost doubled 3 years after clear-cutting (Table 2). Forbs, grasses and sedges, and browse were each more ($P < 0.05$) productive in clear-cut areas than in adjacent uncut areas (Table 3). Of the principal grass species, only bearded wheatgrass (*Agropyron subsecundum*) increased ($P < 0.05$) in the clear-cut. Important dietary

browse species such as aspen and snowberry also increased ($P < 0.05$) following cutting. Production estimates for Engelmann aster (*Aster engelmannii*), American vetch (*Vicia americana*), and western valerian (*Valeriana occidentalis*) were consistently higher in the clear-cut, but were not different ($P > 0.05$) from those in the adjacent aspen forest.

Eighteen years after overstory removal, lodgepole pine clear-cuts were 13 times more productive than adjacent uncut stagnated stands (Table 2). Forbs, grasses and sedges, and browse all increased ($P < 0.05$) following cutting, but mushrooms decreased (Table 3).

Feeding Behavior

In both types, mule deer consumed little or no grass beyond the 1st 2–3 weeks of the season, as compared to the relatively large quantities of grass consumed by elk all summer (Fig. 1; Collins et al. 1978, Deschamp et al. 1979). Deer diets were

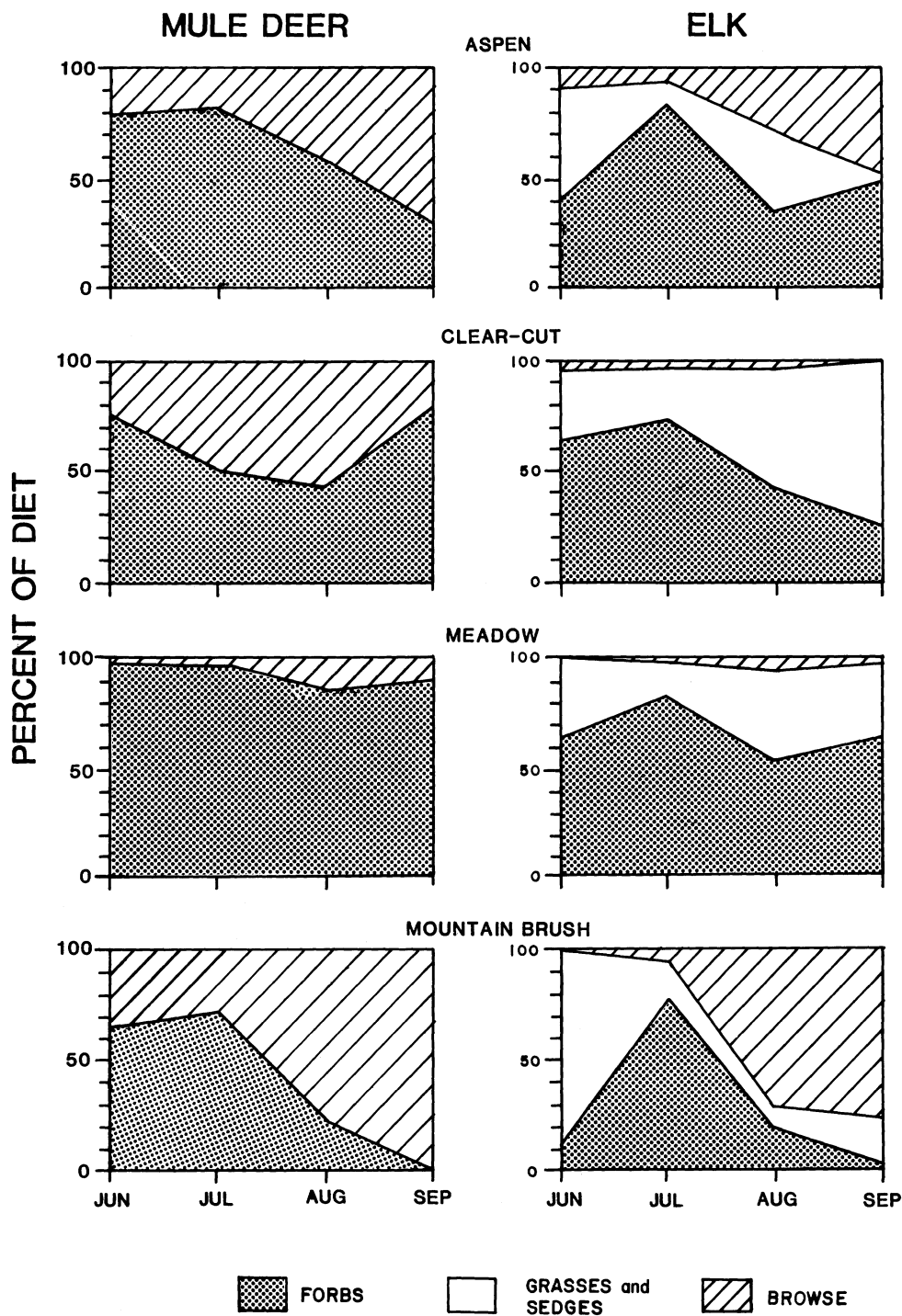


Fig. 1. Mule deer and elk diets by forage class on 4 different habitat subunits in the aspen ecosystem, northern Utah. Percentages are on a dry-weight basis.

Table 4. Mean consumption rates and estimated daily intake (dry-matter basis) by mule deer and elk on different habitat subunits of the aspen and lodgepole pine types in northern Utah.

	Mule deer			Elk		
	Consumption rate (g/min)	Grazing (min/day)	Intake (g/day)	Consumption rate (g/min)	Grazing (min/day)	Intake (g/day)
Aspen type						
Quaking aspen	2.6 a ^a	249	647	11.3 a	99	1,059
Clear-cut	2.1 b	27	59	13.5 b	46	598
Conifer	c			c		
Meadow	2.6 a	216	562	17.2 d	334	5,878
Mountain brush	2.3 b	84	193	15.6 e	49	779
Logging road	c			16.2 e	14	227
Totals		576	1,461		542	8,541
g/kg BW ^{0.75}			73			128
Lodgepole pine type						
Wet meadow	2.7 a ^b	202	545	13.5 a	311	4,196
Dry meadow	2.8 a	21	59	10.6 b	240	2,539
Clear-cut	3.3 b	241	795	9.5 bc	104	989
Mature forest	2.2 c	86	190	6.2 c	24	146
Stagnated forest	1.8 d	110	198	3.7 d	14	52
Revegetated road	ND ^c		ND	8.5 e	21	121
Totals		660	1,791		714	8,043
g/kg BW ^{0.75}			77			156

^a Means within columns followed by a common letter are not different ($P < 0.05$).

^b Consumption rate data for the lodgepole pine type are from Deschamp (1977).

^c ND indicates missing data; however, grazing use of the revegetated road by deer amounted to only 0.5% of deer grazing activity and therefore affects intake only slightly.

generally composed of greater than 50% forbs, with the remainder being browse. Elk also preferred forbs, but to a lesser extent than deer.

Deer consumption rates were highest in the subunits they most preferred to graze: aspen and meadow subunits of the aspen type and the clear-cut of the lodgepole pine type (Table 4). In both types, elk consumed the most forage per unit time in meadow subunits, which they highly preferred as foraging sites. Neither deer nor elk grazed in the unproductive conifer stands of the aspen type and both foraged at only marginal rates in the forested subunits of the lodgepole pine type (Collins 1977, Deschamp 1977).

Although consumption rates of deer were lower ($P < 0.05$) on cut than on uncut aspen stands (Table 4), consumption rates of forage classes and species investigated did not differ ($P < 0.05$) (Table 5).

The elk consumption rate was higher ($P > 0.05$) on clear-cut than on uncut aspen stands (Table 4), with mountain brome (*Bromus marginatus*) being consumed at higher ($P < 0.05$) rates, but browse at lower ($P < 0.05$) rates (Table 5).

Deschamp (1977) and Collins (1977) reported overall consumption rates of mule deer and elk, respectively, to be much higher on clear-cut than on uncut lodgepole pine subunits. Reanalysis of their data (Table 6) indicates that deer consumed forbs at higher ($P < 0.05$) rates in cut than in uncut lodgepole pine, but grass at a lesser rate. All 4 important dietary forb species, common dandelion (*Taraxacum officinale*), Pacific aster (*Aster chilensis*), decumbent goldenrod (*Solidago decumbens*), and heartleaf arnica (*Arnica cordifolia*), were consumed by deer at higher ($P < 0.05$) rates in the clear-cut. Elk also consumed forbs at a higher ($P < 0.05$) rate

Table 5. Forage consumption rates (g/min) of mule deer and elk for forage classes and principal species occurring in cut and uncut aspen stands in northern Utah.

Forage classes or species	Habitat subunit							
	Aspen				Clear-cut aspen			
	Deer		Elk		Deer		Elk	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Forb	1.47	0.20 a ^a	5.27	0.30 b	1.26	0.10 a	6.36	0.77 b
Grass	0.01	0.01 a	3.21	1.53 b	0.00	0.00 a	6.68	2.60 c
Browse	1.11	0.46 a	2.91	1.27 b	0.84	0.27 a	0.44	0.17 c
Quaking aspen	0.18	0.06 a	0.50	0.26 b	0.14	0.03 a	0.09	0.02 b
Snowberry	0.80	0.44 a	2.37	1.34 b	0.61	0.26 a	0.05	0.04 b
Engelmann aster	0.07	0.03 a	0.31	0.14 b	0.03	0.02 a	0.44	0.36 b
American vetch	0.24	0.10 a	0.69	0.43 b	0.14	0.09 a	0.14	0.06 b
Western valerian	0.34	0.10 a	0.11	0.06 b	0.25	0.06 a	0.27	0.21 b
Bearded wheatgrass			2.39	1.12 a			1.72	0.38 a
Mountain brome			0.81	0.46 a			4.66	2.37 b

^a Means within rows followed by a common letter are not different ($P < 0.05$).

in the clear-cut lodgepole pine, but mushrooms at a lower rate. The 3 most important forbs in the elk diet (i.e., dandelion, aster, and goldenrod) were consumed at higher ($P < 0.05$) rates in the clear-cut.

Exact body weights could not be obtained for 2 deer and 1 elk used in the study. However, based on known weights and on estimated weights of unweighed individuals, the mean weight of each group of animals was approximated. These data were then converted to metabolic body weight ($\text{kg BW}^{0.75}$), and intake was computed at $\text{g/kg BW}^{0.75}$ (Table 4). Intake by deer was similar between the aspen and lodgepole pine types, but intake by elk was 22% higher in the lodgepole pine vs. the aspen type.

Percent similarity (PS) was calculated as an index of forage selectivity (Tables 7, 8). When all PS values from either type were applied to ANOVA by ranks, deer were more ($P < 0.05$) selective than elk in both types, especially in the meadow subunit.

The greatest percent overlap of deer and elk diets in the aspen type occurred in the mountain brush subunit during the latter

half of summer, when both species were consuming large amounts of snowberry, the predominant species still actively growing (Table 7). Considerable overlap also occurred in the aspen forest and meadow subunits. Dietary overlap was generally greater in the lodgepole pine type, with the clear-cut consistently having the greatest overlap (Table 8).

Elk diets were more ($P < 0.05$) digestible by elk rumen inocula than by deer inocula (Table 9), except for the highly digestible logging road diet. Deer diets were not always more ($P < 0.05$) digestible by elk inocula; when they were, the difference was usually less than the difference occurring in tests of elk diets digested by elk vs. deer inocula. Certainly there were far fewer differences (3 vs. 9). The smallest differences in digestibility occurred with the most digestible diets. Tests of diets during specific periods of the summer (Collins 1979) showed that the greatest differences occurred in late summer.

Elk generally consumed diets somewhat lower in percent crude protein than deer did (Table 10). Monthly means of

Table 6. Forage consumption rates (g/min) of mule deer and elk for forage classes and principal dietary species occurring in cut and uncut stagnated lodgepole pine stands in northern Utah. Reanalysis of data reported by Deschamp (1977) and Collins (1977).

Forage classes or species	Habitat subunit							
	Lodgepole pine				Clear-cut			
	Deer		Elk		Deer		Elk	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Forbs	1.17	0.16 a ^a	1.01	0.23 a	3.08	0.02 b	8.00	0.72 c
Grass	0.39	0.07 a	1.20	0.68 b	0.16	0.03 c	1.18	0.38 b
Browse	trace	a	1.39	0.58 b	trace	a	0.77	0.37 b
Mushrooms	0.19	0.10 ab	5.87	1.84 c	0.03	0.02 a	0.30	0.14 b
Heartleaf arnica	trace	a	0.19	0.10 b	1.16	0.11 c	0.04	0.02 b
Pacific aster	trace	a	0.00	0.00 a	1.00	0.15 b	1.91	0.28 c
Goldenrod	0.00	0.00 a	0.06	0.02 a	0.22	0.06 b	3.83	0.24 c
Dandelion	0.70	0.17 a	0.00	0.00 b	0.15	0.08 b	1.98	0.50 c
<i>Carex</i> spp.	0.22	0.05 a	1.12	0.67 b	0.11	0.01 a	0.96	0.28 b
Quaking aspen	0.00	0.00 a	0.74	0.34 b	0.09	0.02 a	0.22	0.08 b
Grouse whortleberry	0.36	0.07 a	0.59	0.26 b	0.03	0.01 b	0.04	0.02 b

^a Means within rows followed by a common letter are not different ($P < 0.05$).

both species were above 15% in June and July and generally exceeded 10% in September.

DISCUSSION

In practice, it is extremely difficult to assemble all information pertinent to an explanation of any 1 example of habitat selection. Obviously, this study did not address the entire scope of factors associated with habitat selection by mule deer and elk. It does, however, help document the importance of certain environmental factors to these animals.

Grazing Behavior

Mule deer were significantly more forage-selective than elk. In all but the clear-cut aspen stand, deer selected diets from fewer species in a given subunit than elk did. Generally, both species exhibited the lowest degree of selectivity in subunits with lowest plant diversity or where choice was otherwise limited. For example, mountain brush and mature lodgepole pine subunits mainly produced snowberry and grouse whortleberry (*Vaccinium scoparium*), respectively, and the costs of foraging on less abundant species apparently

Table 7. Selectivity and dietary overlap of deer and elk grazing different habitat subunits of the aspen type, Davis County Experimental Watershed, Utah. Values are percent similarity (*PS*) estimates relating percent dry-weight composition of species in deer and elk diets to percent dry-weight species availability (for selectivity) or relating percent dry-weight composition of deer and elk diets to each other (for overlap). High *PS* values indicate low degree of selectivity or high overlap.

Subunit	Jun			Jul			Aug			Sep			Means		
	Selectivity		Over-lap	Selectivity		Over-lap	Selectivity		Over-lap	Selectivity		Over-lap	Selectivity		Over-lap
	Deer	Elk		Deer	Elk		Deer	Elk		Deer	Elk		Deer	Elk	
Aspen	26	34	23	21	35	41	35	35	59	36	32	42	29	34	41
Clear-cut	25	27	17	27	39	15	40	29	24	36	27	10	32	31	17
Meadow	11	22	46	21	23	43	21	43	26	13	40	18	16	32	33
Mountain brush	24	17	16	28	47	32	53	65	81	46	60	78	38	47	52

Table 8. Selectivity and dietary overlap of deer and elk grazing different habitat subunits of the lodgepole pine type, Uinta Mountains, Utah. Values are percent similarity (PS) estimates relating percent dry-weight composition of species in deer and elk diets to percent dry-weight species availability (for selectivity) or relating percent dry-weight composition of deer and elk diets to each other (for overlap). High PS values indicate low degree of selectivity or high overlap.

Subunit	23 Jun-16 Jul				7 Jul-20 Jul				21 Jul-3 Aug				4-17 Aug				18-31 Aug				1-14 Sep				Means			
	Deer	Elk	Over-lap		Deer	Elk	Over-lap		Deer	Elk	Over-lap		Deer	Elk	Over-lap		Deer	Elk	Over-lap		Deer	Elk	Over-lap		Deer	Elk	Over-lap	
Wet meadow	7	27	51		4	18	57		9	16	54		9	18	53		9	32	39		9	38	19		8	25	46	
Dry meadow	25	41	24		29	37	35		28	40	37		29	45	42		28	43	40		32	40	34		29	41	35	
Clear-cut	31	27	76		26	25	72		26	24	78		28	25	54		25	34	70		26	48	61		27	31	69	
Mature forest	48	86	52		33	76	41		34	65	43		22	33	47		27	31	48		31	45	53		33	56	47	
Stagnated forest	28	37	51		22	37	51		10	37	51		19	29	16		18	31	16		64	37	55		27	35	40	

prevented their being selected at a rate much greater than their random occurrence in the path of the animal. Low selectivity was also exhibited in the dry meadow subunit, where the density and low profile of vegetation apparently made selection of individual plant species difficult for either ungulate. Selection of specific plant parts was not objectively studied. However, deer were observed to be more discriminating than elk in plant parts consumed. Discrimination may have resulted, in part, from restrictions in bite size, e.g., a deer may be able to fit only the terminal half of an American bistort (*Polygonum bistortoides*) leaf readily into its mouth, whereas elk can easily ingest the whole leaf. Conversely, large mouth size relative to the size of plants being browsed may have impeded greater selectivity by elk (Van Soest 1980). In many instances, deer fed exclusively on leaf vs. stem, or leaf vs. petiole.

Contrasts in selectivity may also reflect differences in digestive capacity that dictate the type of forage that can be used efficiently by deer or elk. Van Soest (1980) concluded that ruminants exhibiting greater dietary selectivity have relatively low digestive efficiency, because their ability to digest fiber is inferior to that of true grazers. That elk diets were usually better digested by elk than by deer inocula may be, in part, because elk rumen microorganisms possess the cellulolytic enzymes necessary in the digestion of the fibrous portion of grasses (Leege et al. 1977). The grass portions of elk diets were more digestible by elk than by deer, although not to the extent that would account for differences between deer and elk digestibilities of whole diets. Therefore, other features of the diets must have also contributed to the species differences in digestibilities. Elk consumed relatively more of the structural plant parts (stems,

Table 9. Mean in vitro organic-matter digestibility values (%) of mule deer and elk diets in aspen and lodgepole pine types of northern Utah. Diets were fermented with inocula from both species in separate trials.

Type and subunit	Deer diets		Elk diets	
	Deer inocula	Elk inocula	Deer inocula	Elk inocula
Aspen				
Aspen forest	65.8 a ^a	68.7 b	65.1 a	67.2 b
Clear-cut	71.3 a	72.2 a	63.0 b	68.3 c
Logging road	ND ^b	ND	70.8 a	72.6 a
Meadow	65.7 a	67.3 ab	69.1 b	72.6 c
Mountain brush	70.0 a	72.0 a	67.0 b	71.5 a
Lodgepole pine				
Wet meadow	64.9 a	64.9 a	49.8 b	57.8 c
Dry meadow	61.3 a	62.1 a	60.9 a	68.2 b
Clear-cut	62.3 a	59.9 b	66.6 c	70.3 d
Mature forest	54.7 a	56.6 b	51.4 c	53.5 d
Stagnated forest	57.8 a	58.5 a	57.1 a	64.4 b

^a Means within rows followed by a common letter are not different ($P < 0.05$). LSD = 2.4 for comparisons of means within the aspen type; LSD = 2.5 for the comparison of stagnated forest elk diets; LSD = 2.0 for comparison of the deer diet–elk inocula mean with the elk diet–deer inocula mean; LSD = 1.4 for all other overall mean comparisons.

^b No data available.

twigs, petioles) of shrubs and forbs than did deer, apparently as a direct result of taking larger bites. Schoonveld et al. (1974) demonstrated that mule deer have smaller rumen-reticula, omasa, and abomasa than either sheep or goats of comparable size. They concluded that this characteristic of deer digestive physiology prevented fibrous food from remaining in the rumen long enough for adequate digestion of lignified fiber and that, consequently, large, abrasive food particles passing out of the rumen led to severe digestive upset and food impaction in the omasum. Thus, the differences between in vivo digestibilities of the same diets by deer vs. elk should

be even greater than the in vitro differences, because food would be retained in the elk rumen longer than in the deer rumen. These observations help explain the lower degree of selectivity by elk and indicate that elk will more successfully compete with deer under poor range conditions because they have a greater digestive capacity and wider food base.

The crude protein content of mule deer and elk diets on summer range observed by Pallesen (1979) and ourselves was greater than maintenance requirements and generally in excess of 15%, the level considered necessary for good growth of white-tailed deer (*Odocoileus virgini-*

Table 10. Crude protein ($N \times 6.25$) content (%) of mule deer and elk diets on different subunits of the aspen type, Wasatch Mountains, Utah.

Subunit	Jun		Jul		Aug		Sep	
	Deer	Elk	Deer	Elk	Deer	Elk	Deer	Elk
Aspen	32.7 a ^a	26.8 b	21.8 c	18.7 cd	16.7 de	15.0 ef	12.3 f	12.3 f
Clear-cut	28.8 a	26.2 a	18.4 b	17.8 b	15.2 bc	12.9 cd	14.8 bc	9.9 d
Meadow	21.4 a	22.0 a	18.9 ab	17.7 bc	14.2 cd	15.7 bcd	16.3 bc	11.8 d
Mountain brush	26.3 a	25.8 a	18.1 b	16.9 bc	12.9 cd	10.7 d	10.8 d	10.0 d

^a Means within rows followed by a common letter are not different ($P < 0.05$).

anus) (Dietz 1965, Murphy and Coates 1966); requirements for elk appear to be lower (Nelson and Leege 1982).

In both vegetation types, the estimated intakes (g/kg BW^{0.75}) of elk were much greater than those of deer (Table 4) even though the digestibilities of the 2 species' diets were similar. Estimates of intake for deer in our study appeared realistic compared with the range of 40–90 g/kg BW^{0.75} Cordova et al. (1978) considered acceptable for livestock. Recalculation of data presented by Papegeorgiou (1978) suggests a similar maintenance intake requirement of 80 g/kg BW^{0.75} for red deer in pens. It is possible that much of the difference in our estimates of intake between deer and elk resulted from error in the method of estimation. However, several recent reports have shown that wild ungulates can have intakes greatly exceeding 90 g/kg BW^{0.75}, particularly in summer with diets exceeding approximately 65% dry-matter digestibility. Fulgham (1978), by the chromic-oxide method, estimated intake rates of 102 and 96 g/kg BW^{0.75} for mule deer grazing on sagebrush (*Artemisia* spp.)–grass range in early and late winter, respectively. Westra and Hudson (1981) measured intake by penned elk calves from October through June and found the highest intake (112.8 g/kg BW^{0.75}) during October. White and Trudell (1980) estimated peak intakes for reindeer (*Rangifer tarandus*) of 99–137 g/kg BW^{0.75}. Most recently, C. C. Schwartz et al. (unpubl. rep., Alaska Dep. Fish and Game Fed. Aid Proj. W-121-2, 1981) measured intakes of mature moose (*Alces alces*) equal to 104 g/kg BW^{0.75}. The elk used in the lodgepole pine phase of our study were still actively growing and physiologically comparable, in terms of relative basal metabolic requirements, with the calves used by Westra and Hudson (1981). The high intakes estimated for

elk, mule deer, reindeer, and moose may indicate that some wild ungulates are better adapted to capitalize on high feed availability than are domestic species.

Mule deer and elk use of subunits within aspen and lodgepole pine types was different from their relative availability. In either the aspen or lodgepole pine types, areas further than 60 m from forested edge were not grazed, indicating that they were less acceptable than areas near cover; day or night, both deer and elk quickened their pace while crossing large open areas. Also the animals preferred to graze within the shade of edges during hot clear days. Revegetated roads incurred greater use by elk than by deer. With the exception of the logging road, these subunits represented the most forage-productive areas in their respective types, suggesting that deer and elk prefer feeding in areas where they can obtain the most forage per unit of time. Clary and Larson (1971) likewise concluded that elk may prefer areas of greater forage availability, because their distribution in the ponderosa pine (*Pinus ponderosa*) type in northern Arizona was directly related to total herbage production and forb production. Conversely, they determined that deer distribution was "rather diffuse" and not correlated with forage production. This does not necessarily mean that deer distribution was any less dependent on food supply than was elk distribution, but may indicate that deer feeding-area preference was more closely aligned with aspects of food other than with total herbage production.

Deer and elk in our study had higher consumption rates on subunits they most preferred to graze than on less preferred subunits. Thus, the animals obtained the most food per unit time on the preferred sites. However, deer and elk differed in grazing-area preferences on all but the conifer and logging road subunits, suggest-

ing forage production per se is not the sole factor affecting feeding-site selection.

Arnold (1964) and Bell (1969) reported the amount of forage available to an animal was greatly reduced when closely associated with large amounts of unused herbage. Interference by unpalatable species was greatest when the preferred species were relatively sparse and of low stature in the general vegetal profile. Thus, forbs buried deep in a grass-sedge sward are of limited accessibility to selective feeders like deer, which effectively use only a small amount of mature grass and sedges in their diet. This phenomenon was evident in observations of deer grazing meadow subunits. When grass-like species were accidentally prehended with forbs, they were dropped. Presumably this is why deer, consuming a greater proportion of forbs in their diet than did elk, secondarily preferred the meadows as foraging areas. Clear-cut lodgepole pine areas produced fewer forbs, but because plant cover was much less dense, forbs were more accessible.

The fact that the animals did not graze preferred subunits exclusively suggested that a daily cost-benefit approach to maximization theory (McCleery 1978) did not adequately explain feeding-site selection. The amount of time spent grazing "less productive" subunits exceeded the degree of error Sutherland and Mackintosh (1971) suggested was acceptable on the basis that an animal will make some mistakes in value perception. Bitterman's (1975) theory on matching likewise failed to explain grazing use of apparently suboptimal subunits because estimated digestible dry-matter consumption rates regressed on grazing-subunit preferences yielded significant correlation only in the case of elk grazing the lodgepole pine type. Consequently, the observed pattern of grazing use by deer and elk is probably best ex-

plained in terms of both proximate and ultimate consequences of the behavior. For example, it is likely that natural selection has favored an animal that is motivated to explore its environment as a hedge against possible changes in the environment. In the short term, exploratory animals may receive low-grade reinforcement for their behavior because success at discovering new food sources is enhanced. A new food source may simply result from: (1) forage value relative to other sites improving with the season, (2) complete use of forage at other sites, or (3) animals being behaviorally excluded elsewhere.

Microclimate, particularly the radiation climate, also appeared to affect feeding-site selection. Thermal cover (Thomas et al. 1979, Peek et al. 1982) may influence deer and elk preference for uncut aspen over cut stands. Clear-cuts provided twice the forage of the aspen forest, were free of slash, and had good hiding cover, but lacked thermal cover. Horsefly attacks (Collins and Urness 1982), which were related to temperature and density of vegetation, seemed to have some influence on elk feeding-area preferences.

Resting Behavior

Aside from their preference for edges, elk generally bedded near the spot where grazing ceased. Whether or not the elk directed their feeding pattern so grazing concluded in a certain place is not known. Bedding, following grazing in the meadow, most often was within a few meters of the adjacent edge. Often the animals bedded just outside the edge, but rarely did they bed in direct sunlight. Deer, in contrast, preferred bedding in specific areas and were observed to use the same beds repeatedly throughout the summer. This preference for specific resting sites may represent predator-defense behavior;

greater familiarity with resting locale and possible escape routes may be more essential for a solitary deer than for gregarious elk, which benefit from group surveillance of surroundings. Thermal cover apparently is important for both deer and elk, because centers of clear-cuts (having good escape cover, but poor thermal cover) were not used for bed sites. In the aspen type, horsefly attacks exerted particular influence on resting behavior and may have even determined the range the elk would occupy during the fly season (Collins and Urness 1982).

Deer and Elk Competition

Cliff (1939) concluded that elk would continue to be more productive than deer on poor winter and summer range in the Blue Mountains of Oregon because they can use a wider array of forages. Bird, as cited by Kramer (1972), reported that white-tailed deer populations in Manitoba are much lower in the presence of elk than in elk-free areas. Similarly, Cairns (1976) found that white-tailed deer were more abundant in areas where elk were excluded. However, most discussion of deer and elk competition is inferential, speculative, and controversial (Mackie 1976).

The results of this study do not provide any direct evidence of mule deer and elk competition, because populations were not manipulated or monitored for changes in productivity. However, data on the feeding niches and digestive capacity of the 2 species indicate there is considerable potential for exploitative competition between them favoring elk. In both vegetation types, the feeding niche of elk overlapped and was wider than that of deer. Elk were less selective of plant species and they also ingested older and coarser plant parts. The relatively restricted nature of deer diets represented actual physiological limitations; deer could not

digest some forages as efficiently as elk. Rates of forage consumption by deer were apparently restricted by interference from unpalatable species or plant parts as well. Thus, deer were not capable of using the highly productive meadows to the extent that elk were. This is in agreement with Mackie (1970), who found that elk could more intensively use most plant communities, topographic sites, and all forage classes than could mule deer.

MANAGEMENT IMPLICATIONS

The strong differences in habitat subunit preferences and uses exhibited by mule deer and elk indicate that specific components of habitat should be recognized in the management of either species. The broad classification of a vegetation type as to habitat value is too general to recognize the specific animal-habitat relationships that affect deer and elk. It is also important to recognize that deer and elk differ in their responses to specific modifications or alternative uses of the habitat (i.e., their environments are different although they share the same habitat).

Recent studies (Patton and Judd 1970, Marcum 1975, Black et al. 1976, Lonner 1976) have shown that mule deer and elk make disproportionately greater use of drainage bottoms and areas near water; however, these studies have not identified the exact nature of this relationship. We observed deer and elk to have limited need for drinking water in either the aspen or lodgepole pine types. Apparently, the attraction of the wet meadows was the availability and high-quality of plants associated with high water tables. This was true for both species, but especially for elk. Gentleness of slope appeared to have little influence on the preference for bottoms. This is in agreement with Julander and Jeffery (1964), who found that elk dis-

tribution on summer range in central Utah was affected by only steep slopes. They also reported that mule deer had a slight preference for slopes greater than 30%.

Lodgepole pine and aspen meadow bottoms provided the bulk of forage consumed by elk and approximately one-third of the forage consumed by deer. Thus, meadows warrant special consideration, especially because they are highly susceptible to disturbance in that they commonly represent the most favorable terrain in which to build roads, campgrounds, and summer homes, and to graze livestock.

Riparian habitat is of great importance to big game in unlogged or unburned lodgepole pine forest, where overstory thickening results in lowered forage production of poorer quality. Exclusion of deer and elk from meadow bottoms is probably less detrimental in aspen areas, where adjacent plant communities apparently meet deer and elk habitat requirements, and in lodgepole pine areas, where openings are created by logging or fire. However, some management effort in controlling uses of riparian areas will greatly enhance this valuable habitat for animals using either type. Natural meadows, if well managed, are self-perpetuating and do not require periodic reestablishment as do created openings. There is perhaps more potential for enhancement of big game habitat through alteration of the uses of the landscape than through alteration of the landscape itself (Allen 1977).

The results of this study indicate that potential use of wet meadows by wild mule deer and elk may be greater than previously supposed. At least 3 explanations are possible: (1) because the study animals were accustomed to human activities, they were undisturbed by such activity and made greater use of wet meadows than did their wild counterparts; (2)

during these studies, livestock use was excluded or at minimal impact levels; and (3) the techniques used in this study more directly and accurately accounted for the relative distributions of the animals than do the commonly used techniques that record only the "signs" left by the animals (Collins and Urness 1979, 1981).

If competing uses in aspen or lodgepole pine types limit forage supply, clear-cutting could be used to increase forage production. However, as Pengelly (1972) cautioned, overstory removal is not necessarily beneficial to big game in all situations. Due to the limited and fixed availability of highly productive natural openings in the lodgepole pine type, creation of small openings in extensive, unproductive timber stands would be of value to both deer and elk. This is especially true when livestock grazing or other human-generated activities eliminate a major portion of the forage resource in wet meadows. This assumes no increase in livestock numbers. With low stocking rates, full access to meadow bottoms, and limited inter- and intraspecific forage competition, clear-cutting may be of little value to big game in the aspen type. Although these clear-cuts were less preferred than adjacent aspen stands, they were used periodically throughout the day, suggesting that they are still marginally acceptable habitat. This, combined with greatly improved forage production following timber removal, indicates that clear-cutting of aspen may be beneficial to big game when range conditions are more restrictive. This should be determined before clear-cutting is justified on the basis that it will benefit big game.

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